

GROWTH AND FORM OF FINSPINES IN HYBODONT SHARKS

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ABSTRACT. Hybodontiform finspines have certain diagnostic features. The following are the most important: the longitudinal (axial) ornament is costate apically but tends to break up basally; there are posterior hook-denticles (probably secondarily fused to the spine, because abnormalities include partial non-sequence of denticle rows, also supernumerary denticles); osteodentine of the finspine outer layer is layered anteriorly, and this is interpreted in developmental terms. In common with other finspines, much of the spine was covered by an integument in life, and a certain amount of wound-healing was possible.

THE primitively phalacanthous order Hybodontiformes (*sensu* Maisey 1975) includes such forms as *Hybodus* and *Acrodus*, *Asteracanthus* (*Strophodus*), *Lonchidion*, *Lissodus*, and certain Palaeozoic fishes including *Tristychius*. This arrangement is based on differences in finspine morphology from those of other phalacanthous sharks, a criterion not previously applied, although it offers an apparently natural division. Hybodonts and ctenacanth were recognized as separate, but without clear distinctions (e.g. Schaeffer 1967; Miles 1971). Their finspines are similar in gross morphology but consistently differ in certain structural details. Hybodont finspine structure sets the group apart from all other phalacanthous sharks. The ancestors of modern spiny sharks cannot therefore have been hybodonts, but probably stemmed from a ctenacanth stock.

Material. All specimen numbers quoted refer to the British Museum (Natural History).

Geological range of hybodont sharks. The earliest remains of well-preserved hybodonts are from the lower Carboniferous. These include *Tristychius* and other (as yet undescribed) fishes from the Calciferous Sandstone of Scotland. The group is represented in the Permo-Trias by sparse remains of *Arctacanthus*, *Lissodus*, and teeth and finspines of *Hybodus*, *Acrodus*, and *Asteracanthus*. Hybodonts were gradually replaced by modern sharks from the Jurassic onwards. At the end of the Cretaceous *Hybodus* and *Acrodus* were extinct but *Asteracanthus* may have lingered into the Palaeocene (Tate 1894; Chapman and Pritchard 1904). The group therefore probably became extinct during the early Tertiary.

Gross morphology of finspines. Hybodontiform finspines are elongate and gently curved posteriorly. There are sharp hook-denticles on the posterior wall, usually in two series (Plate 72, fig. 1). Denticles on certain Wealden finspines from virtually a single median series. This is derived from two series in which alternate denticles are suppressed on either side of the posterior midline (Patterson 1966). A ridge is sometimes present between the adjacent denticle rows. Where the series are closely spaced, this ridge winds between the alternating denticles. There is considerable variation in denticle distribution. The denticles are always confined to the posterior

surface of the finspine, never extending on to its sides. Ctenacanthiform finspines (*Ctenacanthus*, *Sphenacanthus*, etc.) lack large posterior denticles. Instead, small denticles lie in postero-lateral series on the spine sides. Euselachian finspines usually lack any form of tuberculation.

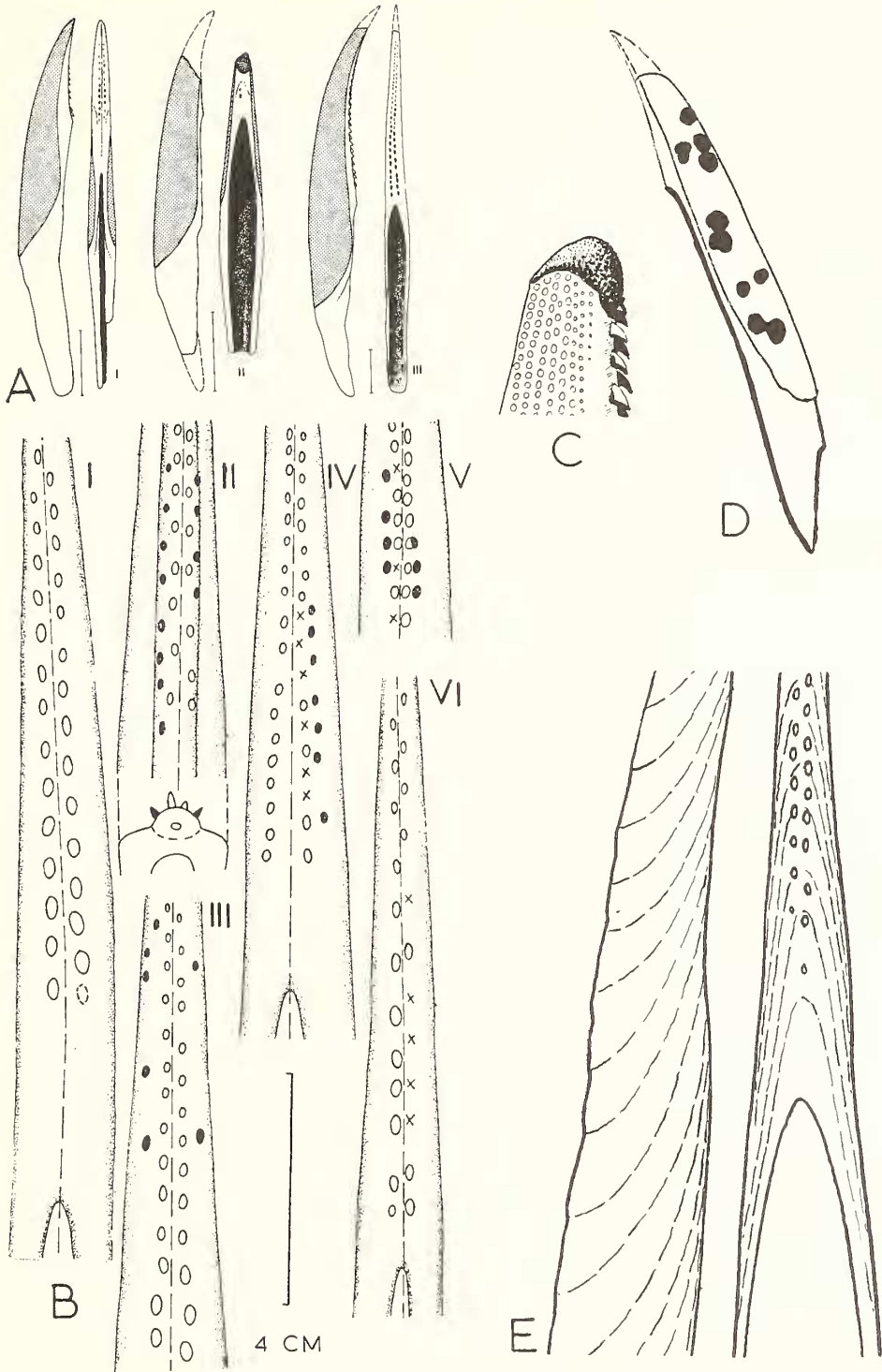
The remaining spine ornament is longitudinally arranged, forming ribs (costae) in *Hybodus*, *Acrodus*, *Lissodus*, and Palaeozoic forms (including *Tristychius*). The tuberculate ornament of *Asteracanthus* is arranged in longitudinal series (Stromer 1927; Peyer 1946). In this form, however, short lengths of costae are sometimes developed coaxial with the tubercle rows, especially near the spine apex (Plate 72, fig. 5). In *Hybodus* and *Acrodus* the costae are sometimes broken up into short lengths, even into tubercles, at their lower ends (Plate 72, fig. 4). To generalize, the antero-lateral ornament is generally costate nearer the spine apex, even in *Asteracanthus*, and is often broken up nearer the spine base, even in *Hybodus* and *Acrodus*. Seen this way, the difference between *Asteracanthus* and *Hybodus* finspine ornament is small.

As the finspine grew, this axial ornament would have been extended basally. The foregoing observations suggest that the growth pattern of hybodont finspines could change from a juvenile (costate) one to a later (tuberculate) pattern. This transition occurred early in *Asteracanthus* ontogeny, but only occurred in very old (possibly gerontic) *Hybodus* and *Acrodus*. *Asteracanthus semiverrucosus* Egerton is an interesting example of a half-costate, half-tuberculate finspine (see Egerton 1854, 1855; Woodward 1916, fig. 8).

The unornamented spine base coincides approximately with that part which is inserted in the body, as with all selachian finspines. The basal opening extends up almost to the lowest posterior denticles. This level is highly variable, as is the shape of the opening (text-fig. 1A). Above it the spine is approximately oval in cross-section. The posterior wall is convex, with denticles near its midline. In euselachians and ctenacanthids this area is flat or slightly concave and devoid of denticles.

The anterior ornament of *Hybodus*, *Acrodus*, and *Asteracanthus* finspines is usually sharply divided off from the rest of the spine. Only rarely, e.g. in *Tristychius* and lower Cretaceous finspines described by Patterson (1966), does the ribbing lack a well-defined lower limit. Costae invariably extend further anteriorly than postero-laterally, and are sometimes interrupted by nodal points indicating pauses in growth. Numerical increase of axial units (costae or tubercle rows) is effected by bifurcation of earlier units, and by intercalation of new units between older ones. Bifurcation or intercalation almost always occurs at nodal points. Adjacent nodes of neighbouring costae correspond to growth lines on the enamelled ornament of euselachian finspines.

TEXT-FIG. 1. A, variation in extent of ornament and level of posterior closure in finspines from: (i) *Hybodus obtusus* P6886; (ii) *H. marginalis* P11921; (iii) *Acrodus nobilis* P2819. B, variation in posterior denticles: (i) normal: *Asteracanthus ornatissimus* P6867; (ii) duplication, both rows: *Hybodus* sp. 32548; (iii) supernumerary denticles, both sides: *Asteracanthus ornatissimus* 40318; (iv) supernumerary denticles and partial non-sequence: *Hybodus obtusus* P6887; (v) partial non-sequence and duplication of rows: *Hybodus* sp. 41222; (vi) partial non-sequence, one row: *H. acutus* 41400. C, D, *Asteracanthus ornatissimus* P12521 finspine; C—apex, showing wound-healing; D—right side, showing circular lesions. E, *Hybodus* sp. 39852; growth lines in lateral and posterior views, with unrelated denticle distribution.



A few specimens actually display growth lines, e.g. 39852 (text-fig. 1E) and *H. brevicostatus* P13268 (Patterson 1966, pl. 3, figs. 1 and 2).

Abnormal finspines. Several specimens have unusual denticle arrangements. Part of either row can be missing (*H. acutus* 41400, text-fig. 1B, vi, *Asteracanthus* P2210), or even an entire row. Where denticles are absent, the opposite row is not necessarily affected. Both rows can simultaneously or alternately lack denticles, e.g. P13268.

Some finspines have partial denticle rows in addition to the primary pair, or even an isolated supernumerary denticle (text-fig. 1B, ii-v). Of these examples, P6687 and 40318 are particularly interesting as they display both non-sequence of denticles in the primary rows, and supernumerary denticle rows in apparently random fashion.

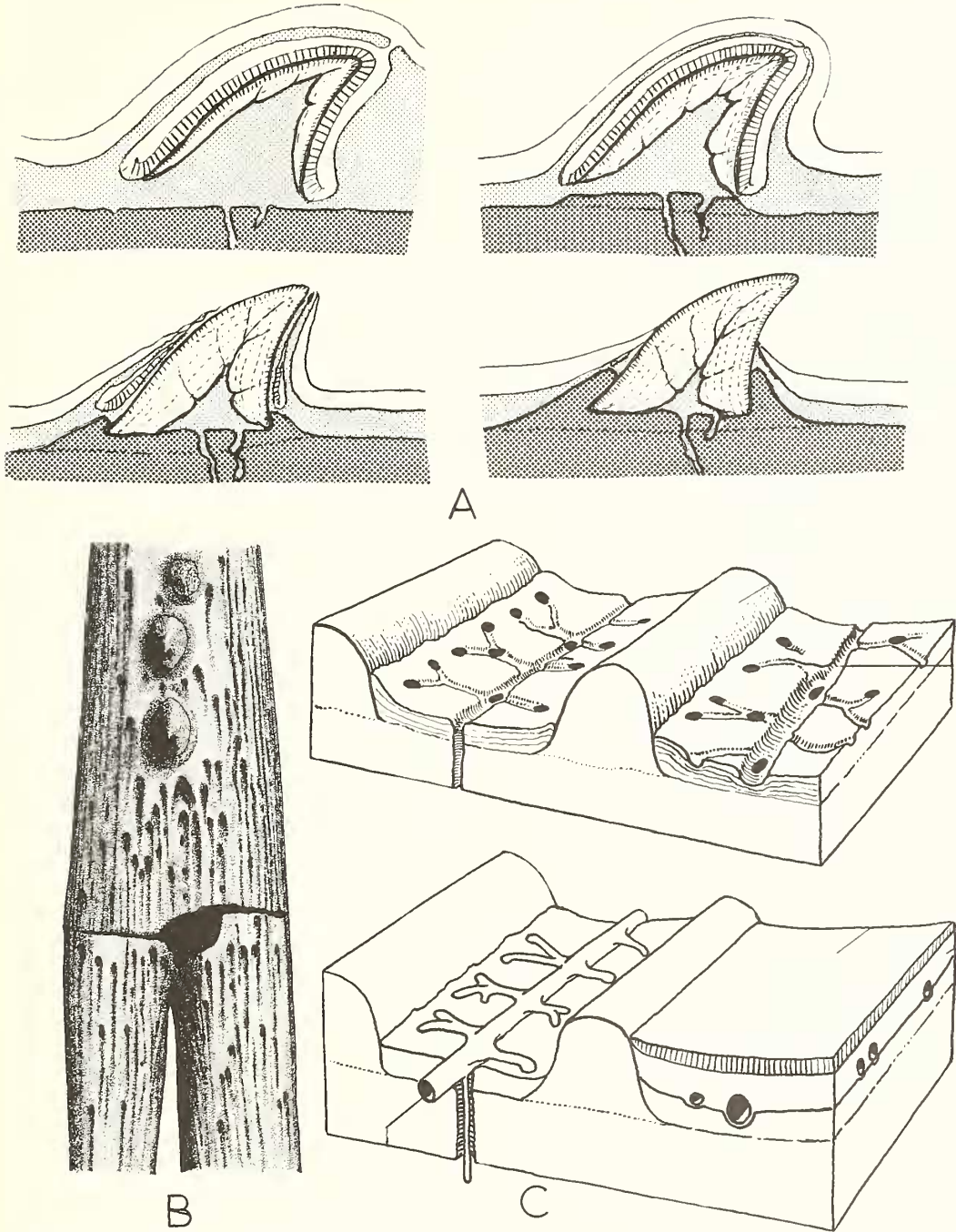
These unusual examples demonstrate the independence of denticles from the rest of the spine. Variation in their arrangement suggests that they are secondarily attached to the finspine as it grows (text-fig. 2A). This process was presumably disrupted in the abnormal specimens, since the finspines are otherwise normal. Further evidence of secondary fusion of denticles to the finspine is found on 39852 (text-fig. 1E). Here, some denticles lie on growth lines, while others lie between them. Denticle formation is not therefore correlated with periods of spine growth, but is irregular.

Injuries and repair. Circular lesions are developed on the spine sides of P12521 *Asteracanthus* (text-fig. 1D). The ornament is stripped away to expose underlying osteodentine. These lesions were probably acquired in life, for they are restricted to the exerted part of the spine; none is seen on the inserted part. Although lesions occur on both sides of the spine, they do not match, and are therefore likely to represent bite-marks. They may, however, have been made by an unknown, superficially attached, and possibly parasitic organism.

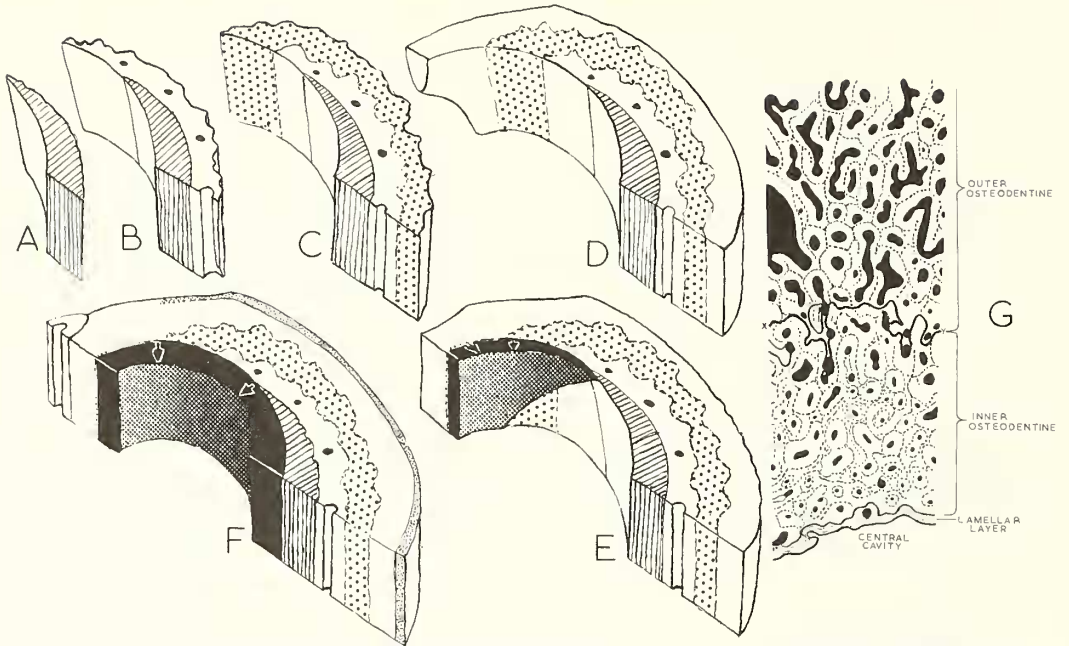
Sessile armoured Cirripedia, e.g. *Xenobalanus*, sometimes develop on squalid finspines and other shark dorsal fins, but are not parasitic (Barnes 1963). Parasitic cirripeds (orders Acrothoracica, Rhizocephala, and Ascothoracica) are devoid of calcareous plates, but today only infest invertebrates. A hybodont finspine would have provided a firm substrate and steady nutrient supply for a parasite. By contrast, thickly enamelled modern selachian finspines would better withstand parasitic attack.

Jaekel (1890) described a damaged *Acrodus nobilis* finspine in which there is evidence of extensive wound-healing. P12521 (*Asteracanthus*) displays similar injury and wound-healing at its tip. There are massive deposits of dentine which partly enclose at least one posterior denticle. Several centimetres of the spine apex have evidently been lost (text-fig. 1C, D). Scleroblastic tissue must have been present at the apex to allow wound-healing to take place.

Internal structure of the spine trunk. The trunk is the main body of the finspine. It includes the unornamented lower portion and also spine tissues at higher levels which are overlain by ornament. There is an outer, highly vascularized osteodentine layer, within which a lamellar layer with few canals is developed apically. Many longitudinal canals run along much of the spine length through the osteodentine, and are linked to each other by a complex system of irregularly branching transverse and radial canals. The longitudinal canals have a semi-ordered arrangement in concentric series



TEXT-FIG. 2. A, diagrammatic sequence showing secondary attachment of denticles to fin spine; B, *Hybodus brevicostatus* P13268; detail of posterior wall, showing denticles surrounded by smooth osteodentine; C, diagrams of intercostal grooves (above) in outer trunk osteodentine (shown layered), with cutaneous veins interpreted (below) beneath epidermis (vertical shading).



TEXT-FIG. 3. A-F, progressive development of finspine trunk (diagrammatic); note late development of inner (lamellar) dentine (in black); G, detail of section shown in Plate 72, fig. 8; there is a major structural interface running between 'inner' and 'outer osteodentine'; the inner layer clearly pre-dates the outer.

(text-fig. 3; Pl. 72, figs. 6, 7). The largest longitudinal canal lies anteriorly. It is flanked by successively smaller ones, but the median posterior ridge which sometimes runs between denticles also contains a large canal (Pl. 72, fig. 7). The lamellar layer is penetrated by radial canals which lack any fibrous trabecular framework. These link osteodentine canals, which do have a trabecular framework around them, to the spine central cavity. The spine surface is pitted by hundreds of pores where canals emerge from the spine. Those emerging between costae or tubercles are joined up by shallow intercostal grooves, giving the impression of a subcutaneous vascular network (text-fig. 2C; Pl. 72, figs. 2, 4, 5). This can be traced down to the level of spine

EXPLANATION OF PLATE 72

Figs. 1, 2. Hybodontiform finspine, Lower Carboniferous, BM(NH) unregistered specimen; *Tristychius?* sp. 1, apex of spine with two denticle rows. 2, lower unornamented part, showing intercostal grooves (for cutaneous veins?).

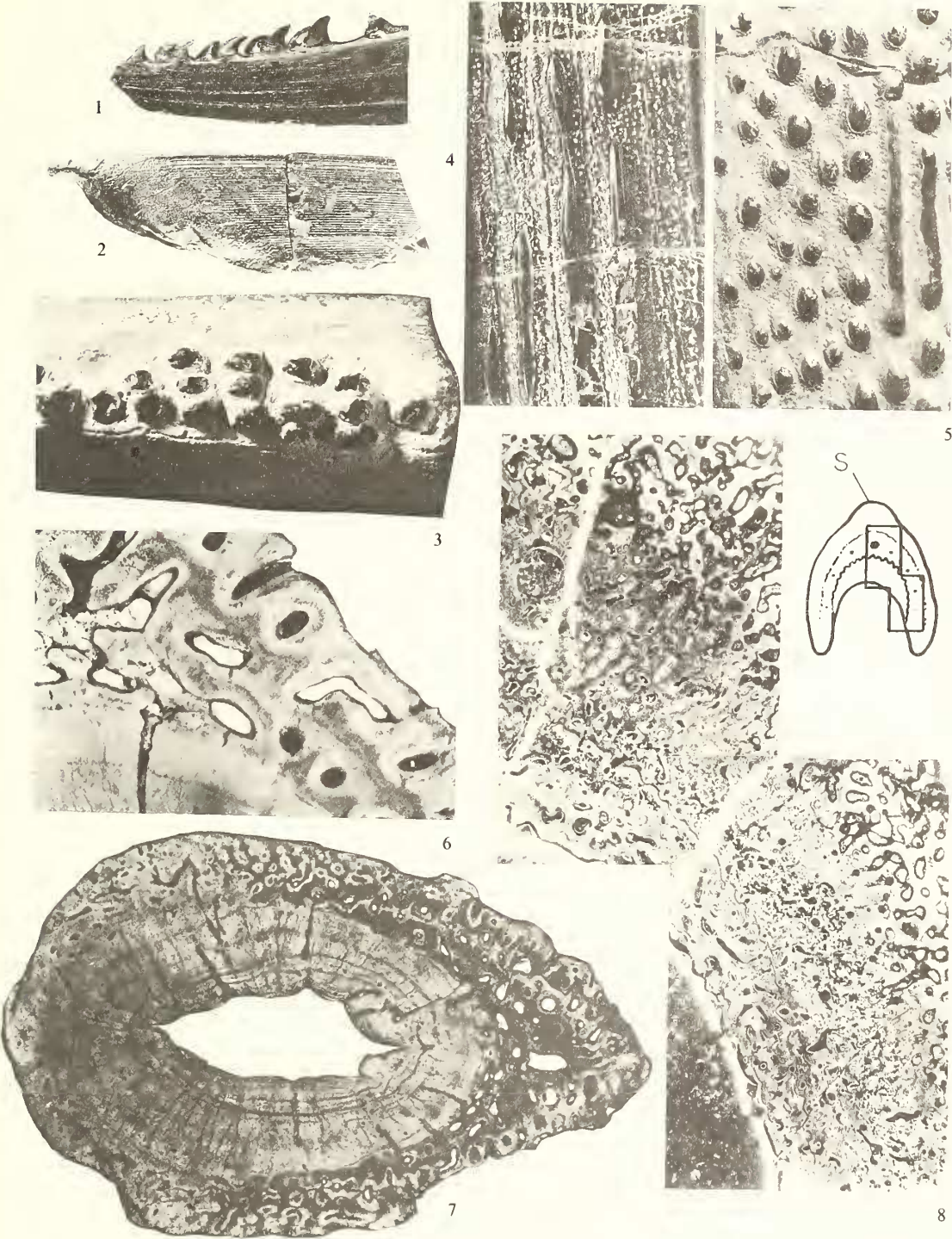
Fig. 3. *Hybodus* sp. 41222 finspine posterior denticles; both primary rows partly duplicated.

Fig. 4. *Acrodus nobilis* P38543; detail of costae broken up into elongate 'islands' and surrounded by intercostal trunk dentine with intercostal grooves.

Fig. 5. *Asteracanthus ornatissimus* P2210; detail of tubercles with short costae coaxial with tubercle rows.

Figs. 6, 7. *Lonchidion?* sp. P47208; finspine transverse section above level of posterior closure. 6, detail of layered osteodentine. 7, complete section (anterior to right).

Fig. 8. *Acrodus curtus* BM(NH) unregistered specimen; detail of layered osteodentine in transverse section (area outlined in inset; s = saddle).



MAISEY, hybodontiform shark fin spines

insertion; below this, pores over the surface produce a more spongy appearance. The major longitudinal canals within the osteodentine emerge at the surface much nearer the spine base, except for the posterior one, which opens just above the level of posterior closure.

The trabecular osteodentine is stratified or layered in transverse sections, except very near the spine base, and shows that dentine apposition was centrifugal (i.e. the newer layers lie outside the older rather than inside them as in a pulp cavity). Sharp structural interfaces resembling irregular growth rings and prominent colour-banding help to define successive dentine layers (Maisey 1975, fig. 1). Layering is less pronounced in the posterior region, but consideration of the shape of superficial growth lines explains this. Anteriorly, centrifugal thickening of the spine occurs at right angles to the spine's major axis, whereas posteriorly dentine is deposited more obliquely to that axis. In transverse section, the anterior region resembles a tree trunk sawn straight across whilst the posterior region resembles a more oblique slice. This also explains why the junction between trabecular and lamellar dentine is clearer at the front than at the back. Lamellar dentine is centripetally deposited, as in a tooth pulp cavity. Topographically it corresponds to the inner layer of euselachian finspines (Stromer 1927; Maisey 1975) but is only present above the level of posterior closure.

Trunk development. The oldest part of the spine is its apex; newer dentine formed at its base. In addition, earlier-formed dentine was secondarily thickened by deposits of newer dentine within canals and in the central cavity. Text-fig. 3 shows diagrammatically how the spine trunk may have grown. The series A-F could either represent successive levels within a finspine (if A-F are imagined to get progressively smaller) or a developmental sequence at a single level (with A-F the same size; ontogenetically earlier parts of the spine will have thicker deposits in the adult than in the juvenile, simply because dentinogenesis is also an ongoing process independent of spine growth).

The trunk base displays the simplest structure (text-fig. 3A) and consists only of newly formed osteodentine. At progressively higher levels (or later stages), other layers of osteodentine overlie the original layer, thickening the trunk walls so that its transverse profile changes, particularly just below the ornament base. This thickening has been termed a 'saddle' (Maisey 1974) because it saddles the earlier deposits and provides a basis for the anterior ornament (Pl. 72, fig. 8). A saddle is more evident in some finspines than in others, possibly providing a means of distinguishing anterior and posterior spines. In articulated *Hybodus hauffianus* the saddle is more prominent in the (more erect) posterior spine. Topographically and structurally the saddle corresponds to the anterior carina of certain euselachian finspines (e.g. *Etmopterus*, *Centrophorus*), because in each case the anterior ornament is developed upon an outgrowth of the trunk outer layer.

Finspine insertion. Articulated *H. hauffianus*, *H. fraasi*, *Lissodus*, and *Acrodus* have anterior finspines inserted at about 35–45° to the vertebral axis. The posterior spine is more erect (up to 75° from the vertebral axis). Finspines terminate basally just above calcified neurapophyses, and partly enclose a triangular basal cartilage (Woodward 1915, fig. 4). Finspine ornament probably continued just below the level of insertion, as in modern sharks. This area would have been overlain by scleroblastic tissue and

by cutaneous veins draining the intercostal grooves. It is likely that at least the intercostal regions and much of the posterior face were covered by soft tissue, first because numerous vascular canals open here, and secondly because limited apical wound-healing was possible. The posterior denticles may have been surrounded by epithelium, as in sting-rays (Halstead 1970), but cannot have been a particularly effective striking organ (Evans 1924). The spine was rigidly inserted and incapable of being used in the same way as a sting-ray spine. The dorsal fin would also interfere with the spine's offensive capability.

CONCLUSIONS

Hybodontiform sharks can best be recognized by the finspine morphology. Their teeth are well known, but few complete dentitions are available. Those which have been described illustrate enormous dental variation, and the form-genera *Hybodus*, *Acrodus*, and *Asteracanthus* may require amendment or even suppression as further discoveries are made. For example, it is impossible to distinguish between *Hybodus* and *Acrodus* finspines, so all forms having teeth and finspines of this type are best regarded as close relatives.

Very few distinct species can be recognized with certainty. Similar taxonomic problems occur with modern carcharhinids. *Asteracanthus* (*Strophodus*) consistently differs from other hybodontiforms in its dentition and finspine ornament. However the different dental arrangement may simply be related to dietary specializations, while the finspine ornament has been shown here to be an ontogenetic variation on a basic pattern. How closely *Asteracanthus* and other Mesozoic hybodontiforms are related is therefore rather uncertain, although a fairly close relationship seems most likely.

Earlier (late Palaeozoic) hybodontiforms have similar finspine structure to their Mesozoic descendants, and the group seems fairly distinct from other sharks in the early Carboniferous. Further study of Palaeozoic forms is required before anything more definite can be said about the origins of the group. It is apparent from other finds that modern phalacanthous sharks are not descended from hybodontiforms, but rather from a more ctenacanth-like ancestor (Maisey 1977).

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